

SIR WILLIAM MACLEAY MEMORIAL LECTURE.  
TIMING IN HUMAN EVOLUTION.

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(Seven Figures.)

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SIR WILLIAM MACLEAY.

Mr. President and members of the Council: Your invitation to deliver a lecture in commemoration of our greatest benefactor tempers any inclination to personal pride with a diffidence compounded of anxiety to do justice to that wise and far-sighted man, and humility at the poverty of what I have to offer. I can only say how deeply I appreciate the honour you have done me.

A first memorial lecture should be a simple recital of the man's life and achievements, an appreciative analysis of the benefits that have ensued upon his generosity and a just picture of him as a man. This apparently straightforward task is fraught with some difficulties. We know something of his life, and his public achievements are officially recorded. The fruits so far of his benefactions are apparent in the flourishing state and reputation of the Society, in the quality of the papers published in the PROCEEDINGS, in the records of the Linnean Macleay Fellows, and so on. But of Macleay personally we know only that his great modesty forbade practically any intrusion of himself into public affairs. What little we know of him we gain from the opinions of others, and those I have read have invariably been high ones.

What little is known, indeed, has been avidly seized upon by all previous commentators in an attempt to present a worthy appraisalment. Haswell (1891), Fletcher (1893 and especially 1920 and 1929), Walkom (1925, 1942) and others have gobbled up every scrap, leaving little for a successor. Lately Macmillan (1957) has expanded a small morsel into his delightful book on the *Chevert* expedition but it seems unlikely that many more such morsels will give themselves up. Consequently, I must tell the well-known story in my own way, acknowledging that I have drawn freely on the authors I have cited. Also, largely because the story is so well known, I feel that much of the detail can safely be left for reference to their works. My account of Sir William Macleay is, therefore, relatively brief, and I shall supplement it with a short discussion of some matters that have interested me during the last few years.

William John Macleay, like any other living organism, cannot properly be assessed apart from his environment. It was the context of his surroundings, current events and personal contacts—especially family ones—that brought out those particular features that cause us to honour him tonight. Macleay's context, appropriately enough, takes us back to Linné himself so perhaps I might start at that point.

Elsewhere (Abbie, 1954) I have discussed briefly the influence of Linné in the early history of Australian biology. That depended largely upon his association with Sir Joseph Banks through Solander, Dryander and Fabricius. When Linné died Banks was offered the entire Linnean collection of books, specimens and cabinets for one thousand guineas (Smith, 1911). Banks did not purchase but a young Dr. Smith was persuaded to do so. The collection reached England in 1784 and Smith was moved to found a *Linnean Society*, which was established in London in 1788. Banks took great personal interest in the new society and defrayed many of its early expenses—an example followed even more generously a century later by the subject of tonight's talk.

*Alexander Macleay.*

The story now really begins for, six years after the Linnean Society of London was founded, the first relevant Macleay entered upon our scene. In 1794 Alexander Macleay was elected a Fellow of the Linnean Society and in 1798 he became its second secretary, a post he held until 1825.

Alexander Macleay was born in 1767 in the County of Ross; his father was Provost of Wick and Deputy-Lieutenant of the County of Caithness. Alexander held various public offices from 1795 until 1818, when he retired on a pension at the age of fifty-one. In 1825 the Earl of Bathurst persuaded him to come to Australia as Colonial Secretary, which position he filled until 1836. Alexander was elected the first Speaker of the (old) Legislative Council in 1843 and carried out his duties with ability, judgement and impartiality until 1846, when he retired because of his age. Two years later he died in his eighty-first year.

From his first association with the Linnean Society Alexander had collected biological material—chiefly insects—in Britain and from other countries by exchange or purchase. His collection, already famous before he left England, formed the basis of the Macleay Museum. He does not seem to have published any scientific papers but was elected a Fellow of the Royal Society in 1809 and a Councillor in 1824. In Australia (although some material was sent to the Linnean and Zoological Societies of London) collecting appears to have languished somewhat in favour of horticulture, in which Alexander gained high regard; but he was an ardent supporter of the Colonial—later Australian—Museum. He owned property at Brownlow Hill and Glendarewel Farm in the Camden district, and on a grant of land “near” Sydney (one and a half miles from Sydney Town) built Elizabeth Bay House, which was occupied almost continuously by Macleays from 1837 to 1903.

*William Sharp Macleay.*

The eldest son of Alexander was born in London in 1792 and graduated from Cambridge in 1814. Until 1825 he was in Paris on government service and became friendly with Cuvier, Lamarck and other notable French biologists. Then he went to Havana, Cuba, on a mixed English and Spanish Commission for the abolition of slavery. After occupying various posts there he returned to England in 1836 and retired on a pension the next year at the age of forty-five. In 1838—in the company of his cousins William and John—W. S. Macleay left England for ever to settle in Australia.

W. S. Macleay's first inspiration to biology probably came from his father and was stimulated deeply by his contact with the French biologists. However, he does not appear to have begun collecting seriously on his own account until he went to Cuba. He published a number of papers, including the *Horae Entomologicae*, which contained philosophical speculations on the “Circular System” and “Quinarianism” so misapplied by over-enthusiastic friends that they fell into disrepute. When Macleay returned from Cuba he met Darwin, also newly returned from his famous voyage on the *Beagle*, and was one of those who urged Darwin to publish his diary (F. Darwin, 1887). Macleay was elected to the Councils of the Linnean and Zoological Societies of London and was President of Section D at the 1837 meeting of the British Association for the Advancement of Science.

On the voyage to Australia with his cousins W. S. Macleay collected marine biological material assiduously. In Sydney he warmly embraced the new biological field, especially in ichthyology, and made a wide circle of like-minded friends, of whom, biologically speaking, the most important were Dr. George Bennett and Thomas Henry Huxley. Huxley mentions him as “William Macleay” in a letter from Sydney in 1848, and in 1851 wrote to “W. Macleay” in Sydney on the possibility of a professorship in natural history at Sydney University (L. Huxley, 1900). This publication refers only to “Sir William Macleay” in the index but it is obvious from the context and cross checks that William Sharp Macleay was the person concerned. Curiously, there appears to be no reference to W. S. Macleay in the *Rattlesnake* diary (J. Huxley, 1935).

While W. S. Macleay collected widely and made valuable contributions to taxonomy, his real interest lay with the pre-Darwinian philosophical and systematic side of

biology. A great service to Australia was his strong support of the Australian Museum. He was a member of the Committee from 1841 to 1853; then he was elected a Trustee, a responsibility he sustained until 1862, when ill health forced retirement. He died in 1865 at the age of seventy-three and left most of his possessions to his brother George, then in England. From our point of view it was most fortunate that he bequeathed the whole of his own and his father's natural history collection to his biologically-minded cousin William John Macleay.

*George Macleay.*

George plays a less direct part in this story. The third son of Alexander, he was born in London in 1809 and came to Australia at about the same time as his father. At first he was mainly occupied in managing his father's Camden property with the help of a younger brother James. George also acquired a property of his own on the lower Murrumbidgee. He went with Sturt's second expedition down the Murrumbidgee and Murray Rivers in 1829-30 and distinguished himself on that arduous venture. So early as 1836 he was a member of "A Committee of Superintendence of the Australian Museum and Botanical Gardens" and later was elected a Museum Trustee. George became Member for the Murrumbidgee in the (old) Legislative Council in 1855 (Legislative Assembly in 1856), but he resigned all his appointments when he returned to England in 1859. There he was elected a Fellow (later Councillor) of the Linnean Society and was created K.C.M.G. Some time between 1869 and 1874 he made a brief visit to Australia to help wind up the estate of his brother W. S. Macleay. He married twice but had no children and died at Mentone in 1891 in his eighty-second year.

George collected for his father on the Murrumbidgee but does not appear to have been an ardent naturalist. Nevertheless, the interest was there, as his election to the Linnean Society shows, and his long support of the early Australian Museum merits much commendation. We would consider that his most valuable contribution lay in the guidance and encouragement he gave his cousin during the early days of squatting on the Murrumbidgee, when the future Sir William was founding the fortune that makes the rest of this story possible.

*William John Macleay.*

The chief figure in this account was Alexander's nephew, born at Wick in 1820. At about seventeen he began to study medicine at Edinburgh University but the death of his widowed mother inclined him to heed his uncle's advice to migrate to Australia. William and his brother John embarked with W. S. Macleay towards the end of 1838, reaching Sydney in March, 1839. There was a big family reunion at Elizabeth Bay House. John was delicate and was advised to take a sea voyage—quaint advice in view of the fact that he had just completed one of some months' duration! So he set off back for England but died on the way. Meanwhile, William took up a property—Kerarbury—on the lower Murrumbidgee, no doubt on the advice of his uncle and of cousin George, who was already established there. For fifteen years William experienced the typical life of a squatter, coming to Sydney only as occasion demanded. We know very little indeed of the Murrumbidgee era apart from an episode of great personal heroism in the face of bushrangers. Fletcher (1929) has recounted some details of property transactions at that time but they are too complex to be discussed here. There is no doubt, however, that William prospered. In 1855 he was elected Member for Lachlan and Lower Darling in the (old) Legislative Council. Responsible government was introduced in 1856 and William represented the same district in the Legislative Assembly. When George Macleay departed for England in 1859 William became the Member for the Murrumbidgee until he resigned in 1874. In 1877 he was elected to the (new) Legislative Council and held that seat for the rest of his life. He was an independent but public-spirited parliamentarian, advocating many necessary reforms and serving actively on a number of committees and commissions. He became a Trustee of the Australian Museum—thus preserving the family tradition—and a member of the Senate of the University of Sydney. He was knighted in 1889, two years before he died.

From 1855 on, William's parliamentary duties demanded more and more of his time in Sydney; and on his marriage to Miss Susan Emmeline Deas-Thomson in 1857 he took up permanent residence here—first at Denison House, Phillip Street, and later at 153 Macquarie Street. Thereafter, his Murrumbidgee property was left to the care of a manager. When W. S. Macleay died in 1865, William and his wife moved finally to Elizabeth Bay House.

William's first interest in biology may have been aroused by his preliminary medical studies in Edinburgh. At all events, such interest must have been stirred on the voyage with W. S. Macleay, who pursued biological work *en route*. While on the Murrumbidgee William probably undertook some collecting for his uncle but it seems clear that any biological urge had little opportunity to express itself until he was permanently settled in Sydney, where, in 1856, he became a member of the Philosophical Society of New South Wales. In Sydney he had access to the collections of Alexander and W. S. Macleay (which he inherited on the death of the latter) and began active collecting on his own account. To this end he undertook personal collecting trips, employed collectors in various parts of Australia and arranged exchanges and purchases from overseas. (In 1873 the Senate of the University of Sydney accepted his offer to bequeath the whole combined Macleay collection to the University.) William was largely instrumental in getting the Entomological Society of New South Wales started in 1862. He was the first president (W. S. Macleay having declined because of his health) and contributed a number of papers to the *Transactions*—which journal attracted the attention of entomologists elsewhere. However, the entomological ranks in Sydney dwindled and the Society lapsed after eleven years, the last number of the *Transactions* appearing in 1873.

Workers in wider biological fields were becoming more numerous, and Macleay's own collection and interests had gone far beyond entomology. It seemed that a society less narrowly confined would be a more suitable forum for naturalists generally. In 1874 he recorded that "Dr. Alleyne and Captain Stackhouse are trying to get up a Society of Natural History". This marked an epoch in William's life. He resigned his parliamentary seat and thereafter devoted himself almost entirely to natural history. Perhaps the current visit of H.M.S. *Challenger* helped to determine the issue.

There seems to have been a proposal to call the new society "The Banksian Society". In view of Banks's services to biology in general and Australia in particular that would have been appropriate enough. Nevertheless, the decision to name it "The Linnean Society" was undoubtedly correct. Linné's system of classification provided the firm basis for general biological work; the title is more explicit; Banks himself had been a great supporter of Linné and of the Linnean Society of London; and all the relevant Macleays were at some time Fellows of that Society. On 28th October, 1874, a preliminary meeting in the board room of the Sydney Public Library decided to form the Society, fixed the subscription and chose a distinguished list of officers with William Macleay as president. On 4th November the proposed rules were adopted; on 13th January, 1875, the office bearers and council were formally elected, and on 25th January the first scientific meeting was held in Lloyd's Chambers, 362 George Street.

While all this was in train William had been looking for a vessel to take a collecting expedition to New Guinea and he purchased the barque *Chevert* early in 1875. She proved stout enough but was not suitable for conditions on the New Guinea coast. The story of that expedition has been fully told by Fletcher (1893, 1929) and by Macmillan (1957) so I shall not delay you with the details. To some extent—particularly in the failure to penetrate inland—the expedition fell short of expectations. But, speaking as one who has had to organize more modest expeditions of a different kind, I can say that few, if any, fulfil all the hopes of the planners. That apart, the adventure was a signal success. A large quantity of material was collected, biological interest everywhere was excited and it was shown that Australia could manage an undertaking of that sort quite independently of outside help. Naturally, this enterprise proved a great stimulus to the new Society, to which we must return.

The Linnean Society's changes of fortune and residence have been amply described by Fletcher and Walkom, and by others incidentally. All this I need not go over again. There are, however, some points that stand out and should be emphasized. One is the unwavering generosity of William Macleay in furnishing from his own pocket accommodation, secretarial assistance, help towards publication costs and liberal support in the provision of an adequate reference library. And few societies have enjoyed such munificence as almost complete replacement of the library after the disastrous fire at the Garden Palace, or such a gift as the Linnean Hall at Elizabeth Bay, or such a final bequest as seems to ensure the stability of the Society far into the foreseeable future. In all these respects I feel that William Macleay surpassed even his exemplar Sir Joseph Banks in generosity.

Yet Macleay was no mere Mycaenas. He gave freely to support the science he loved but he was also an active worker in and for that science, whether in the field and laboratory or at the secretary's desk. In all this I think that we can see more than ordinary generosity: it was, rather, an unwavering determination—in the face of setbacks that would have frightened lesser men—that the Society should survive at all costs. But for this, biology in Sydney would have fared badly, for the University had no medical school and, consequently, no school of biology. Macleay, with his far-sighted vision of the importance of biology to Australia's economy, supported what was virtually an extra-mural school until the University repaired its omission. However that may be, there is no doubt that through all these vicissitudes he ensured that workers could continue with their research and publish it without hindrance. In the outcome, the Society grew steadily in reputation, as it has continued to grow since, to its present status of one of the foremost of such societies. To be able to say that is ample justification for this meeting in Macleay's honour.

At that point one should stop but there is a little more to be said. Macleay became a member of the Senate of the University and was appointed to a committee on the setting up of a medical school. This was realized in 1883 and the consequential Department of Biology proved complementary to the Linnean Society, the two combining splendidly to foster still more vigorously their common interests. Macleay took the necessary steps to further that cooperation by leaving his museum to the University and, above all, in establishing the Linnean Macleay Fellowships. One more example of his amazing prescience should be recorded. He was one of the few to foresee the potential importance of the newly founded science of bacteriology and he provided money to support study of that branch of biology too.

When Sir William Macleay died on 7th December, 1891, he left behind the reputation of a great man and a generous benefactor. But he left considerably more—a living, growing memorial in the flourishing Linnean Society of New South Wales, and in the distinguished scientists who owed their first opportunity to the Linnean Macleay Fellowships.

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After that I hesitate to obtrude myself but I take courage from the fact that the eminent contributors to the *Macleay Memorial Volume* of 1893 felt that the best tribute they could offer was an account of their own work. I must apologize that the subject of my further discussion is so commonplace—a single animal, forming a single genus of the Primates and represented by only one species. However, man is part of natural history and I take refuge in the avowed object of the Society: “the cultivation and study of Natural History in all its branches.”

## TIMING IN HUMAN EVOLUTION.

### INTRODUCTION.

In the famous tenth edition of his *Systema Naturae* Linné (1758, p. 20) courageously included man with his most similar contemporaries in the single order Primates. This he did on a purely objective study of physical characters.

That alone was a tremendous advance for which Linné is always to be honoured. But he stopped short at classification, accepting in principle the view that species are *sui generis* and have been so for all time. However, increasing knowledge brought to light forms not so easily pigeon-holed, intermediates that aroused suspicion of some mutability in the living order. The century that followed the publication of Linné's classification saw a great deal of work and speculation on the possibility of an evolutionary process and exactly within the century Darwin and Wallace supplied the first convincing evidence in favour of organic evolution. Then busy minds turned to seek for the underlying mechanism, and so on to the nature of life itself. Another century has passed, some of the mechanisms are becoming apparent and it is the last problem that now arouses the greatest interest (Abbie, 1955).

Here it is not my ambition to probe so deeply. Instead, I wish to draw attention, in a very limited way, to one mechanism—to the element of time (or, rather, timing) in physical development. This is only a part of the problem but it is interesting in itself and can, as I hope to show, give an indication of the sort of thing that has happened—might even afford some indication of what could happen.

In 1916 D'Arcy Wentworth Thompson (see Thompson, 1942) extended the application of mathematical techniques to problems in morphology. His work may be considered the culmination of a purely physico-mathematical school of thought which failed to make allowance for such variables as genetics, adaptation, convergence, etc. Nevertheless, he showed that by manipulation of appropriate Cartesian coordinates it is possible to derive sundry recognizable variants of form—even quite bizarre-looking ones—from well-known basic patterns. These may be considered, in a purely relative sense, distortions in space. Huxley (1932) followed this up with his work on relative growth which gains by taking genetics into account and imports time into the inquiry on such distortions. Medawar (1945) also drew attention to the incidence of time. The progress made along these lines is seen in such publications as *Tempo and Mode in Evolution* (Gaylord Simpson, 1944), *Essays on Growth and Form* (Le Gros Clark and Medawar, 1945), *Growth* (1948) and many others.

It will be appreciated that instances of differential growth are really manifestations of acceleration or retardation in the development of some limited region in respect to the remainder of the body. That is, localized distortions in space could equally be considered localized distortions in time—timing in onset, speed, duration and cessation of growth. Indeed, it is difficult to see how distortions in space could occur apart from distortion in timing. However that may be, it is my intention to consider the effects of timing in development and I shall restrict my remarks chiefly to the animal with which I am most familiar—man.

Before I start I should make a brief comment on the basis of this paper. In 1926 Bolk pointed out that many features of the human skull represent a retention into adult life of characters distinctive of foetal stages of development. This he called “foetalization”. The conception was extended more widely into the animal kingdom by Garstang (1928), de Beer (1940), Hardy (1954) and others, who introduced the terms “paedomorphism” and “neoteny” to embrace this general application. The

reverse process was designated "gerontomorphism". I have used such ideas in considering problems of the human skull (Abbie, 1947, 1952*a*) but in the latter paper I pointed out that not all peculiarly human features can be attributed to paedomorphism: many must be considered the result of gerontomorphism. Schultz (1957*b*) has recently repeated this warning.

Paedomorphism represents a slowing down in differentiation—a delay in timing; gerontomorphism is a speeding up in differentiation—an acceleration in timing. It is the balance between these two in different parts of the body that produces the distinctively human form among primates and, to a large extent, the distinctions of physically different ethnic groups among humans. Clearly it is not possible to consider all the examples of primate paedomorphism and gerontomorphism, even if we knew them, so I must confine myself to a few of the most outstanding.

#### TIMING IN THE HEAD.

##### *The Skull.*

It is well known that the skulls of all major primates are closely similar up to the time of birth (Abbie, 1952*a*). At that stage the calvariae are little more than osteo-fibrous membranes for the brain (Abbie, 1947) and a rudimentary facial skeleton is suspended below. Thereafter differentiation proceeds actively, but at different rates in different animals. In most non-human primates the jaws, in particular, rapidly become large and protuberant and the calvariae may show such developments as big brow ridges and nuchal and sagittal crests, although these features are not necessarily correlated (Abbie, 1952*a*). Human skulls never attain to great extremes. As Bolk pointed out originally: in the skull, and particularly in the relatively large round brain case, the human retains more of the foetal character. In different ethnic groups, of course, suppression of such features varies considerably (Fig. 7), and the same applies within any ethnic group—a European may well have quite big jaws and large brow ridges, an Australian aborigine may have relatively small jaws and a high round forehead (Abbie, 1951). Nor is the shape of the head predetermined and immutable. In 1911 Boas (see Boas, 1940) showed that human headform can change with change in environment and this has since been confirmed by other observers (see Kaplan, 1954). I have shown (Abbie, 1947) that the changes detected by Boas are not haphazard but, in fact, with improvement in environment headform tends to adhere more to the foetal type: neither much longer nor much shorter than the mean foetal cranial index at about the middle of the human scale (Fig. 7). It seems, then, that paedomorphism is still an active factor in determining at least one human character.

Apart from such obvious features, human adherence to foetal standards is disclosed in more subtle ways—generally thinner cranial bones, delayed closure of sutures, tendency to retain a metopic suture, more forward siting of the foramen magnum, more open sphenomaxillary fissure (Hone, 1952), trend towards failure of third molar teeth to erupt, and so on. Also, cranial paedomorphism is accentuated where growth is arrested short of full differentiation as in dwarfs, pygmies and adult females.

Gerontomorphism in the human skull is shown in a number of less obvious features. The relatively high nose has departed more from the foetal standard than has the flatter nose of apes. This may be "adaptive". The mastoid process is usually much better developed than in most apes and here timing is deeply involved: Schultz (1957*b*) points out that the human mastoid process appears soon after birth and is practically maximal by adulthood; in the gorilla mastoid development does not begin until after the permanent dentition is completed and is not finished until old age, when the process is as large as in a young man. In this respect man has far outstripped the ape in attainment of a high differentiation, and this may well be "adaptive"—to provide secure attachment for the sternomastoid muscles which help to hold the head upright.

Particular interest centres upon the jaws, which betray an interesting mixture of paedomorphism and gerontomorphism. Overall, the human jaws are relatively small, a paedomorphic feature possibly aggravating the tendency to suppression of the third molar teeth—from lack of time and/or space to get them through. Perhaps associated

with this is suppression of the premaxillae as separate bones. This may be due either to prenatal closure and obliteration of the premaxillo-maxillary sutures or to overgrowth of the premaxillae by the maxillae (for discussion see Johnson, 1937; Wood Jones, 1938). In either case the result must be considered paedomorphic. It marks a very decided departure from the regular primate pattern and is not, I think, to be dismissed so lightly as Schultz (1957*b*) suggests. In the lower jaw Murphy (1957) has shown that there are two distinct growing parts, an alveolar border and a basal portion, which should be treated separately. Only occasionally do humans show much true facial prognathism—with the jaws as a whole protuberant; but they frequently exhibit some alveolar prognathism—when the alveolar borders and teeth protrude in front of the line of the jaws proper (Abbie, 1952*a*). In this case alveolar growth exceeds basal growth. In apes alveolar (as well as facial) prognathism is marked and the chin is left behind—is decidedly receding, in fact. In man, to a varying extent in different ethnic groups, there is usually a well-marked chin which indicates that basal growth in the mandible has kept up with, or even exceeded, alveolar growth. The absolute amount of basal growth may be less than in apes but the human chin is relatively more advanced and differentiated, and this must be considered an instance of gerontomorphism.

#### *Cranial Capacity and the Brain.*

Human cranial capacity far exceeds that of any other known primate. No gorilla, even one three times the size of a big man, has a capacity much more than some 600 c.c. while the human average is around 1400 c.c. The human range is very wide—from about 800 c.c. (an exceptional minimum recorded by Le Gros Clark, 1937) to well over 2000 c.c.—but within that range size is no index of mental ability, and this includes all putative “missing links”, such as *Pithecanthropus*, *Sinanthropus*, Neanderthal Man and so on, but not the Australopithecinae, which are down towards the ape series.

The human brain is not, of course, absolutely the biggest known—it is exceeded by that of the larger whales and adult elephants. But here the factor of total body bulk intrudes and raises the question of relative brain size. This is determined by the brain weight: body weight ratio. On this criterion the human wins handsomely over all other large brains. In the biggest whale the ratio is about 1:25,000 (Wood Jones and Porteus, 1929), i.e. brain weight is only 0.004% of the total body weight, whereas in an adult human male the ratio exceeds 1:50, i.e. the brain is more than 2% of the total body weight (Vierordt, from Donaldson, 1895). But even in this respect man is not supreme, since the little marmoset (*Hapale*) has a higher ratio, although the brain itself is, naturally, very much smaller.

The human brain, then, is distinguished by two factors—great absolute size and great relative size. What has timing to do with this? That is best determined by comparing growth of the human with that of other primates. For this we may use some figures supplied by Schultz (1957*b*) with the qualification that he relates cranial capacity in cubic centimetres (not brain weight) with body weight in grams (his table 3 and fig. 9). The cranial capacity of the newborn human is 14% of the body weight, and the figure is very similar for the great apes. Apes attain maturity at about 11 years as compared with twice as long for man, yet the apes end up with a cranial capacity of less than 0.25% of body weight whereas the human finishes with a cranial capacity of 2% of body weight. Man shows considerable retardation in physical maturation as compared with apes, and his brain departs much less from the foetal proportion: this may legitimately be cited as an outstanding exhibition of paedomorphism. The point is well illustrated by Vierordt's figures (see Donaldson, 1895, p. 69) which compare the relative weights of all the important viscera at successive stages of human development.

#### BODY AS A WHOLE.

Man shares with other animals an axial growth gradient of cephalo-caudal differentiation during ontogeny (Child, 1915). This is shown first by the large head, tapering trunk and absence of limbs (Fig. 1). As development proceeds, the trunk



becomes distinguishable, then the upper limbs and finally the lower limbs appear, enlarge and ultimately catch up to their proper proportions. That is, the peak of the gradient gradually shifts backwards, and in the limbs similarly moving gradients control proximo-distal differentiation.

For example (Fig. 2), the crown-rump length drops from over 70% to just over 65% of the total stature (crown-heel length) during the last six months of gestation. Vertical head height, which starts near 50%, is only 30% at three months and has dropped to just under 25% at birth. On the other hand, the upper and lower extremities, which appear later, show a second-month acceleration—the upper ahead of the lower—which continues during the third and fourth months and then tapers off—again the upper before the lower. Within the extremities the first spurt is in the proximal segments, which slow down as the intermediate and distal segments

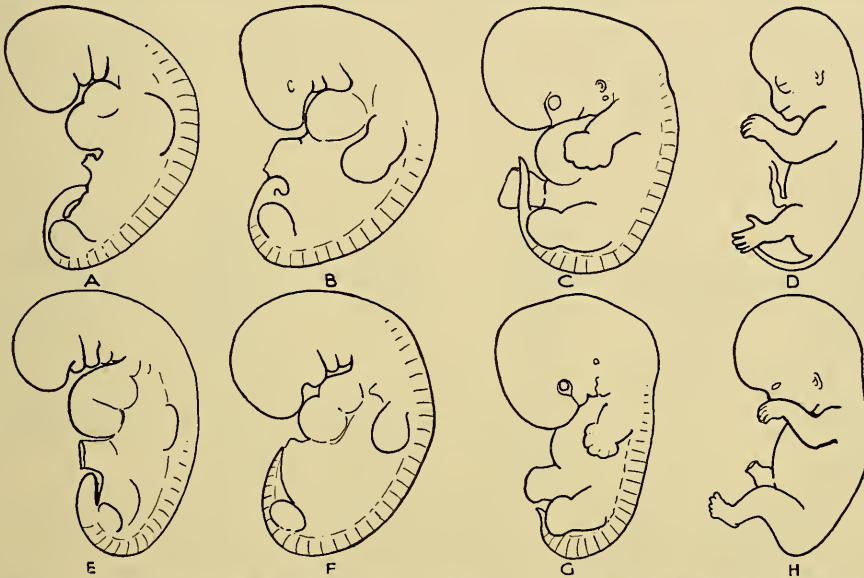


Fig. 1.—Comparative foetal stages: A-D, macaque at 26½ days, 31 days, 36 days and 53 days respectively (drawn from Heuser and Streeter, 1941); E-H, human at 5.2 mm., 7.3 mm. (drawn from Streeter, 1945), 12.2 mm. and 30.7 mm. respectively.

successively take over the impetus and in turn catch up and then slow down (data from Scammon and Calkins, 1929). The process is similar in other primates. Many more illustrations of this distal shift in the growth gradient peak could be given but the point is sufficiently made for our purpose.

It would be convenient to be able to describe this shift in a single word. I had considered, and discarded as ugly, the term “distalization” when I came upon the botanical adjective “acropetal” to express the idea of “extremity-seeking” growth. With your permission I shall import it into zoology.

To continue: By the time of birth the human foetus has a head which occupies nearly one-quarter of its total length, a trunk twice as long but inferior extremities only a little longer than the head (Fig. 3, A). With the passage of time these proportions change. Growth of the head slows down—at six years it is about one-sixth of the total stature and in the adult only just over one-eighth. The changing ratio of brain case to face is also quite notable. Growth of the trunk and upper extremities proceeds at a moderate pace without striking changes. But the inferior extremities pursue vigorously their process of catching up, occupying progressively more and more of the total stature and, in effect, pushing the trunk farther and farther from the ground. In adult European males, in the outcome, the top of the pubis is just above the mid-point and the sitting height is only a little over half the total stature.

Various factors may modify the final proportions. Anything that accelerates maturation or slows down the growth rate—e.g. hypergonadism, malnutrition, achondroplasia, hypothyroidism, etc.—hampers extension of the lower limbs which end up relatively shorter than the norm. This is evident in several kinds of dwarfs, and also in healthy adult females who stop growing some years earlier than males. On the other hand, anything that delays maturation or accelerates the growth rate—e.g. hypogonadism (eunuchoidism), hyperpituitarism—favours extension of the inferior extremities which, to our eyes, become disproportionately long.

However, the European standard of bodily proportions is only one possibility and other ethnic groups may depart from it quite distinctly, while still within terms of the cephalo-caudal gradient. Some, particularly mongoloids in China, Japan, Alaska and South America, whose growing period does not seem to be curtailed, exhibit such slowing down that their inferior extremities are relatively short and they

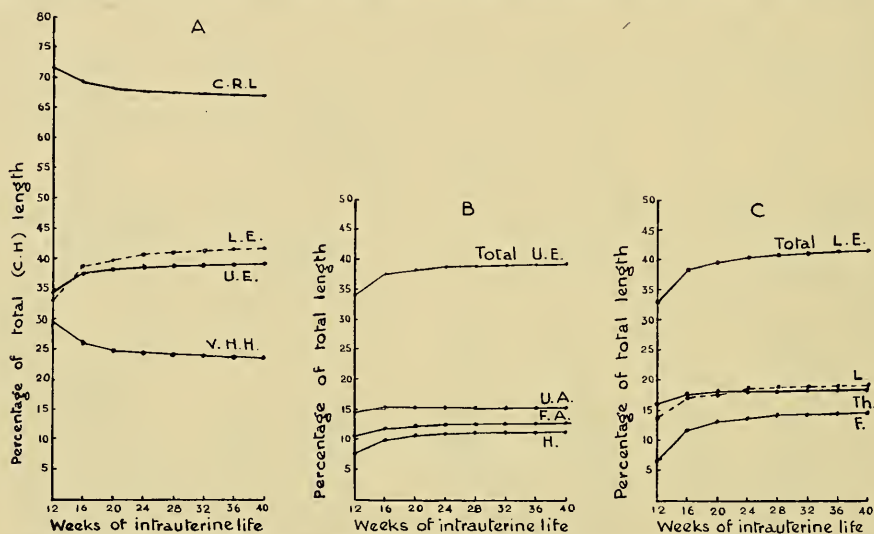


Fig. 2.—Human: Comparative growth of body as a percentage of total (crown-heel) length. A, Body and total extremities; B, Upper extremity; C, Lower extremity. C.R.L., crown-rump length; L.E., lower extremity (total); U.E., upper extremity (total); V.H.H., vertical head height; U.A., upper arm; F.A., forearm; H., hand; Th., thigh; L., leg; F., foot. (Data from Scammon and Calkins, 1929.)

retain more foetal proportions in the trunk and head (Fig. 4). Keith (1919) has attributed this to a sort of ethnic hypothyroidism, but that seems unlikely. On the other hand, many peoples, notably in Africa, within the limits of the normal human growing period achieve so much acceleration that their limbs appear exaggerated in comparison with the trunk and head (Fig. 4). This, Keith has suggested, may be due to hyperpituitarism, but again that is unlikely. The Hottentot woman presents an interesting anomaly. Although she belongs to an almost "pygmoid" group, her extremities, particularly the inferior, are relatively very long. In this case it seems that some "genetic acceleration" overrides the usual picture of dwarfism.

Among long-legged peoples, the most interesting to us are the Australian aborigines. We have now (Abbie and Adey, 1953*a*; Abbie, 1957 and unpublished data) a large collection of measurements and X-rays relating to aboriginal growth which afford some insight on what happens. It is evident from figure 5 that in both sexes the proportion of stature contributed by the inferior extremities in aboriginal adults greatly exceeds that in Europeans. At birth the proportions are about the same in the two peoples (Fig. 3, A and B), and the aboriginal growing period may even be slightly less than the European (Abbie and Adey, 1953). Yet in aborigines of both sexes at about the sixth year the inferior extremities make a sudden spurt to produce proportions com-

parable with those of a European child of twelve. Thereafter extension of the inferior extremities does not appear to proceed any faster than in Europeans. It is the sixth-year spurt, superimposed upon the regular growth pattern, that determines the aboriginal advantage in this respect. Here the matter of timing is clearly important.

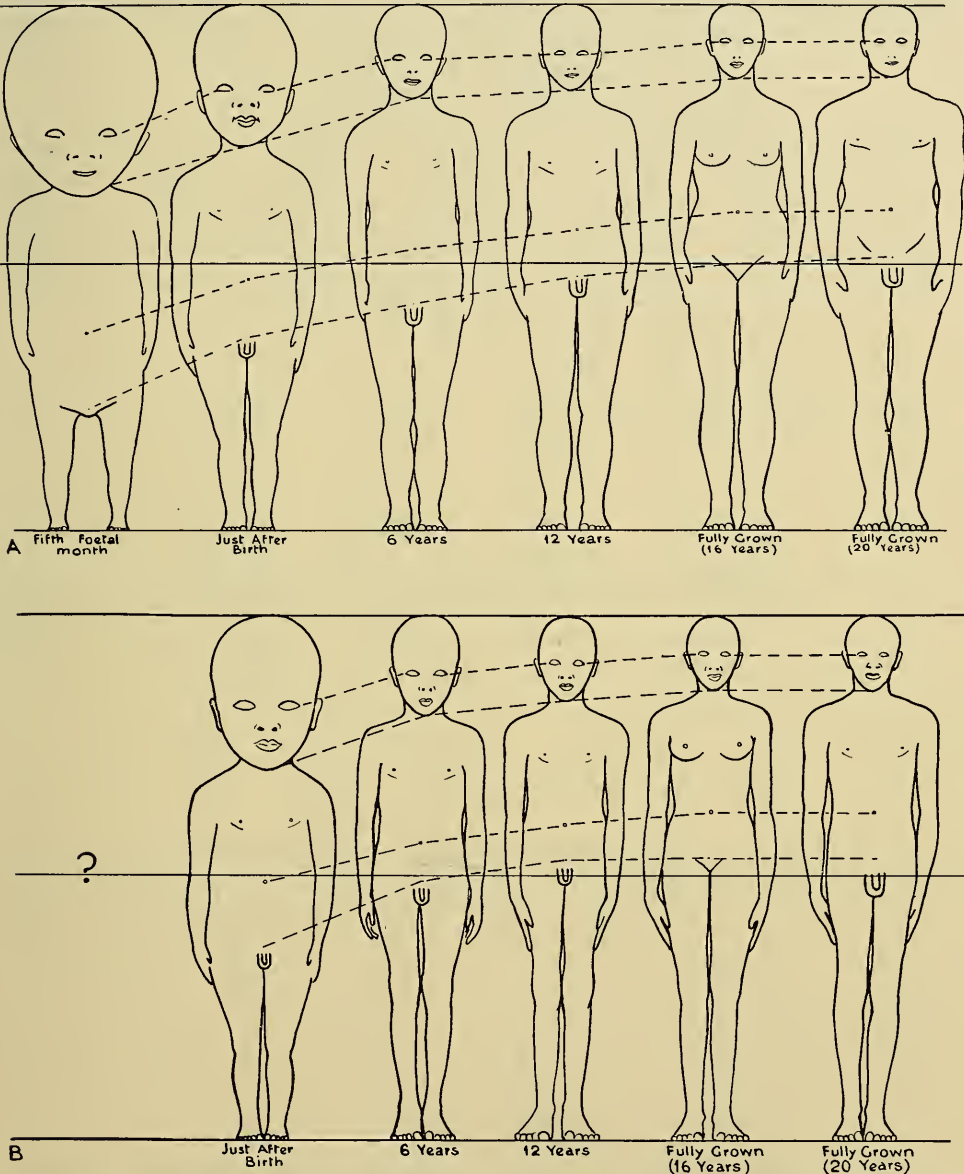


Fig. 3.—Progressive growth pattern in, A, Europeans (redrawn from Abbie, 1950), B, Australian aborigines (personal data).

The European child does show a spurt, but delays it until about the age of twelve, when there is not time enough left to catch up with the aborigine. There do not seem to be sufficient data on other long-legged peoples to determine whether or not they follow the aboriginal pattern.

Acropetalism extends to segments of limbs and, generally speaking, where limb growth as a whole is accelerated in comparison with Europeans, so is growth of the

distal segments, which become relatively longer. The different forms in figure 4 illustrate this sufficiently, particularly in the inferior extremities. The trend is less noticeable in the superior extremities, for in most peoples the tips of the extended fingers fairly constantly reach to just below the middle of the thigh, no matter how long this may be (Figs. 3 and 4). Nevertheless, the trend does exist and is expressed

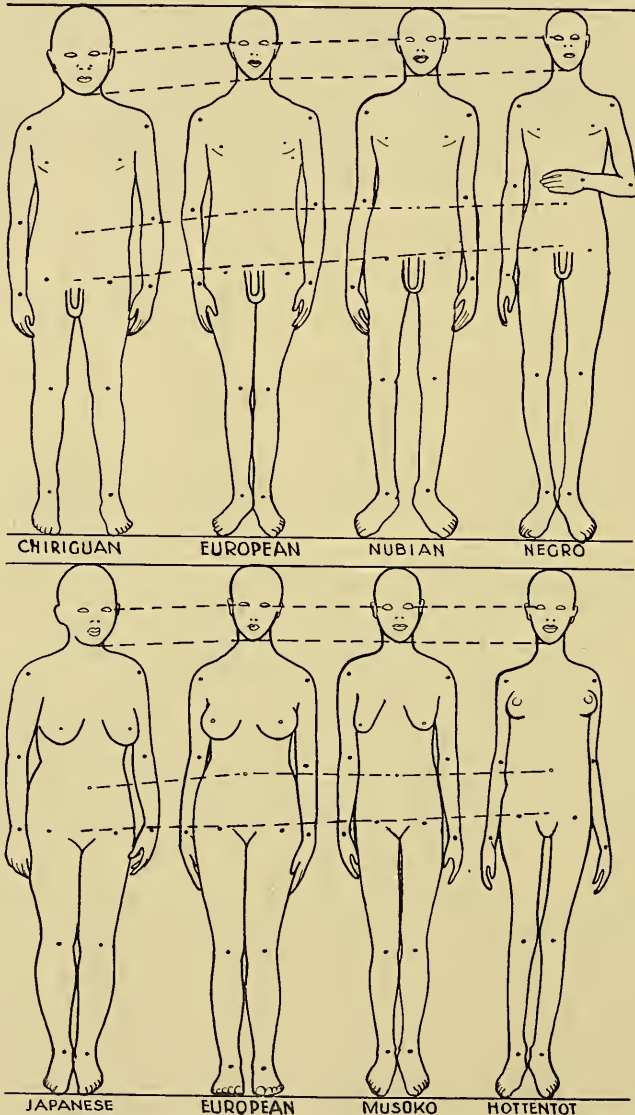


Fig. 4.—Comparison of proportions of various ethnic types, all drawn as far as possible to the same length from photographs in Martin (1928). The dots indicate, so well as the poses permit, the approximate ends of the various limb segments.

as a relatively longer forearm and hand. Conversely, those whose limbs remain short betray suppression of acropetalism in their relatively shorter distal segments.

The great apes present quite a different picture (Fig. 6). Their acceleration is most obvious in the superior extremities, which also show marked acropetalism. In comparison, the inferior extremities are relatively stunted (although acropetalism is evident in the foot: see Schultz, 1949, 1957*a*, 1957*b*, for data). This could be due to

the fact that the shorter growing period (only half the human) limits the time available for extension of the inferior extremities. It is equally likely that the total pattern is genetically determined in "adaptation" to brachiation and the quadrupedal mode of progress imposed by the inadequate feet. At all events, it is clear that embryological timing has emphasized the anterior end of the growth gradient rather than the posterior end. The accent on inferior extremities in the human must be considered an example of gerontomorphism *vis-à-vis* the apes.

TIMING IN OTHER DEVELOPMENTS.

A glance at Table 1 will disclose a number of further features which betray equally well the total slowing up of human development as compared with other primates. Gestation, development of pigmentation and hair, ossification, onset and completion of dentition, growing period and onset of senescence are all progressively slowed down, as we go from monkeys, through apes to man, in whom the trend is outstanding. A number of developmental features indeed—pigmentation, hair growth, dentition—despite the extended growing period, may never reach finality at all.

TABLE 1.

Primate.	Gestation. (Weeks.)	Completion of Pigmentation.	Complete Covering of Hair.	Carpal Ossification Centres at Birth.	First Dentition. (Months.)	Second Dentition. (Years.)	Growing Period. (Years.)	Life Span. (Years.)
Macaque ..	24	Early in gestation.	During gestation.	All centres.	0.6- 5.9	1.6- 6.8	7	25
Gibbon ..	30	} Onset during gestation, completed after birth.	} Onset during gestation, completed after birth.	2-3	1.2- ?	? - 8.5	9	33
Orangutan..	39			2-3	4.0-13.0	3.5- 9.8	11	30
Chimpanzee	34			2	2.7-12.3	2.9-10.2	11	35
Gorilla ..	37			?	3.0-13.0	3.0-10.5	11	35
Man ..	40	(Coloured.) } Onset mainly after birth. (White.) (Never.	} Never completed.	0	6.0-24.0	6.0-20.0	20	70+

Date from Bolk, de Beer and Schultz (slightly modified).

Here I should add in parenthesis that while pigmentation does become complete in some coloured peoples this must be attributed to "natural selection", not to alleged affinities with sub-human primates. In many aborigines completion of pigmentation is delayed until adolescence or later (Abbie and Adey, 1953*b*).

One might add that the tail, so well developed in most monkeys, is suppressed almost to extinction in both the apes and man. That is an example of pedomorphism, but it is also an "adaptive" process, since the remnants of the tail and its muscles are modified to form the pelvic floor which supports the viscera in the upright posture. This is of considerable importance in humans but less so in the more quadrupedal apes. However, such a contrivance does not seem to be always necessary since other orthograde animals, e.g. the kangaroo, manage very well without it.

Although the longer inferior extremities in man represent a manifestation of gerontomorphism, some qualification is necessary in regard to the foot. As is well known, in all non-human primates the great toe is widely separated from the others—like the thumb in the hand—and this feature is established early in prenatal life (Fig. 1). In man the great toe not only lies close to the others, it is firmly attached to them by the deep transverse ligament of the sole (deep transverse metatarsal ligament of Wood Jones, 1944). This is a serious stumbling block to those who would derive the human foot directly from the ape's. It has been claimed that in the mountain gorilla (*G. beringei*) the great toe lies closer to the foot than in the lowland gorilla (*G. gorilla*) and may represent an intermediate stage (e.g. Morton, 1935; Schultz, 1957*b* and others). I feel that this would be hard to sustain. Separation of

the toes depends upon the development of radial splits around the periphery of the footplate (Fig. 1). In non-human primates the split for the big toe extends deeply, releasing a highly mobile organ. In man the splitting is partly suppressed. It is true that in some ape feet a fleshy web extends across the interval but the deep transverse ligament does not include the great toe within its grasp in any primate other than man (Wood Jones, 1944; Raven, 1950). In man, fixation of the great toe is an important factor in preserving orthograde stability and in walking in the upright position. Apes, despite the fact that they may go for limited periods on

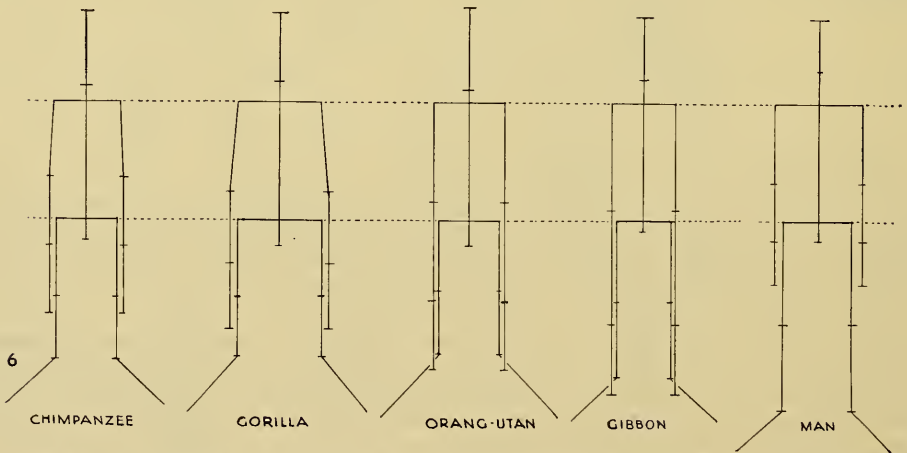
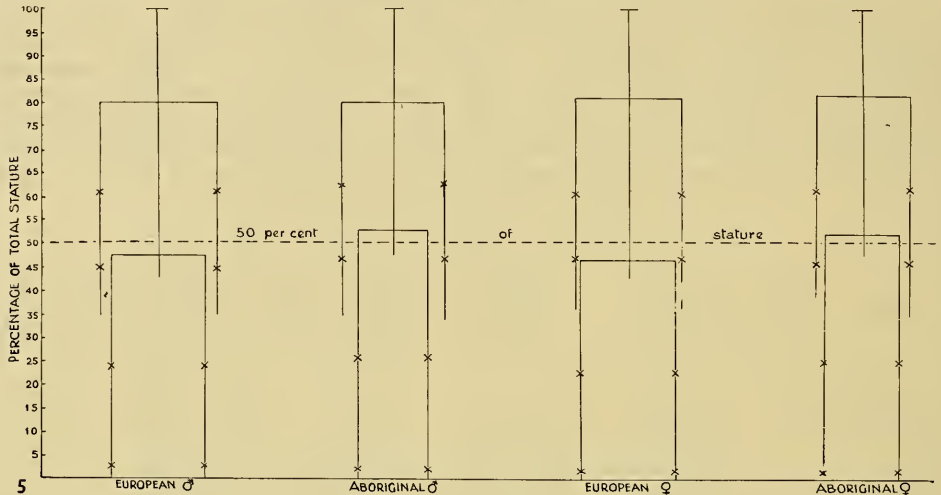


Fig. 5.—Comparative proportion of adult male and female Europeans and aborigines all drawn to the same dimensions (redrawn and modified from Abbie, 1957).

Fig. 6.—Comparative proportion of man and other primates taking trunk length as a common basis. (Redrawn and modified from Martin, 1928.)

their hind limbs alone, are essentially quadrupeds, supporting themselves on their excessively long upper extremities and “walking” upon only the outer borders of the feet. So far as man is concerned, the peculiarity of the great toe is functionally “adaptive”; in our present context limitation of splitting off is an example of suppression in development—paedomorphism. Suppression in development is also exhibited by the other toes, which never become as long relatively as in apes (Schultz, 1957*b*) but leave the “big” toe in a dominant position. On the other hand, modification of the astragalus and os calcis to form the human talus and calcaneum, and so the

human heel, implies a great advance, even upon apes, in differentiation and specialization.

Here there is space only to mention the high grade of specialization in the human vertebral column, sacrum, thorax and pelvis, all in the interests of the upright posture (Schultz, 1957*b*).

#### OTHER CONSIDERATIONS.

A few other points demand attention. Acceleration of growth may lead to high differentiation, i.e. gerontomorphism. But prolongation of growth at a lesser speed may approximate to the same end result and it cannot be denied that prolongation of the growing period really represents retention of the foetal tendency to grow, i.e. it is paedomorphism. Yet it is conceivable that these two diverse processes could produce a similar outcome. How can confusion be avoided here?

I think that the answer lies in considering what is achieved in a given time.

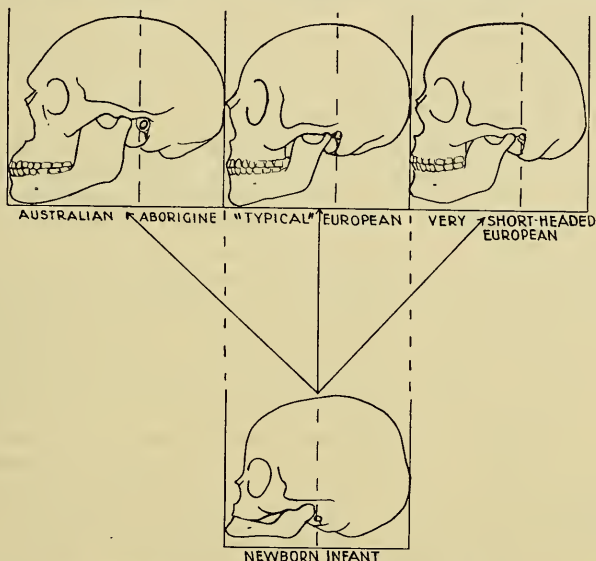


Fig. 7.—Adult human skulls of contrasting types derived from a common foetal pattern.

To take a crude example, a gorilla, in most physical features, including size, has achieved far more differentiation in 11 years than a human has in twice the time. In this respect the human is strongly paedomorphic in comparison with the gorilla *in toto*. Many peoples have longer inferior extremities than Europeans, but so far as can be detected they all achieve that distinction within approximately the same growing period. They are more differentiated in the same time and must be considered in this respect gerontomorphic; those who end up with shorter inferior extremities after an equal period of growth are paedomorphic relative to Europeans. The superior extremities of apes are obviously gerontomorphic in this respect, but when it comes to the inferior extremities as a whole difficulty arises. The apes have much shorter inferior extremities, but they also have a much shorter time in which to develop them. Here it would be rash to decide without qualification whether the apes are paedomorphic or whether "adaptation" outweighs everything else.

Perhaps when comparing animals of different genera it would be wise not to depend too much upon absolute chronology but to introduce some form of physiological chronology. This is a matter that requires more consideration than I have been able to give to it.

A point that has not been discussed in detail is the effect of the environment on the expression of genetically determined characters. The term "adaptation", of course, implies that the environment is involved, but for each animal it is a special

environment. In the case of man I am concerned mainly with the improvement in environment—including particularly nutrition—that has followed the advance of civilization. There is little doubt that our changing environment is producing some physical changes. This is evident, for example, in the increase in stature and weight of modern school children as compared with their parents at the same age, and probably in more subtle ways, such as the change in headform detected by Boas (1940) in the children of American immigrants. Elsewhere (Abbie, 1948) I have considered some aspects of that problem. Here I need only say that we have no idea yet of what is the optimum environment for man—until we have we cannot do more than speculate on what he could become with his present genetic make-up.

For the moment I must ignore any possible effects from increasing radiation.

#### CONCLUSION.

In tracing the development of primates we are watching different expressions of what is essentially the same process. All start off at about the same point but are endowed with different potentialities which become manifest during ontogeny as the imposition of differences in the timing of secondary developments. In one part change starts early and differentiation is advanced; in another it is delayed and differentiation is correspondingly retarded or even suppressed.

Development can be looked upon as a cinematographic film which comprises the whole of differentiation and can be run fast or slow as desired, or at different speeds at different times. When the whole film, or any section of it, is run through fast, development is accelerated, parts rush to completion, many details are blurred or lost, others become exaggerated; nevertheless, much more film can be run through in the time available and in terms of differentiation much more can be achieved. If the film is run through slowly the whole process is drawn out, features are unfolded in great detail and some hitherto unsuspected disclose themselves; however, much less film can be run through before time is up—if the running is slow enough even an extended showing, as in man, is inadequate—and the total achievement in final differentiation is correspondingly reduced. We have no idea of the proper speed for the film, or even its length—although the result seems to be reasonably satisfactory for any particular animal—but it would be interesting to speculate on the results if the speeds were changed. Certainly there is wide scope for variation and so far as man is concerned we get some hints from various developmental disorders and ethnic differences. At all events, the speed is evidently not constant: most animals show retardation in some features, acceleration in others. That applies equally to man but on balance I think that in man, as compared with other primates, the slowing down far outweighs the speeding up. In other words, paedomorphism is the major factor in deciding human peculiarities.

We can say that while paedomorphism sets the basic human pattern gerontomorphic intrusions impose many decisively human specializations. Instances of both may clearly be designated "adaptive". But "adaptation" is only a rather teleological way of saying that some genetically determined characters become emphasized one way or another because that fosters survival in man's particular context. It is noteworthy that this applies not to the characters themselves—which are common to all primates—but to the timing they are accorded during development.

The explanation for man's distinctions, then, is to be found in his genetic make-up, and particularly in that part of it which regulates the rate at which different elements of the pattern unfold. Therefore, when looking for some common ancestor for man and other primates it is necessary to seek among embryos, not adults (Abbie, 1952*a*, 1952*b*). This is simply a special case of von Baer's modification of the Meckel-Serres "law". If I am correct—and I hope that I have persuaded you that I have some reason on my side—man's ancestry and affinities are not to be discovered by comparison of adult primates, particularly when the possibility of convergence is taken into account. Conceivably, a minor embryological twist in any primate stock could introduce the changes in timing necessary to produce the human stem and "selection" would do the rest. Consequently I am sceptical about "missing links" and "sub-human" forms of hominids.



However that may be, it is evident that the features that distinguish man—and men—are, at least largely, due to differences in timing during development. I do not, of course, think that that is the only factor, and I may have over-emphasized its importance. If I am wrong then I can take comfort from Goethe: "Es irrt der Mensch so lang er strebt."

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